

REVISION OF THE GENUS *GOLFINGIA* (SIPUNCULA: GOLFINGIIDAE)

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Abstract.—The species in the sipunculan genus *Golfingia* (*Golfingia*) are reviewed and evaluated in light of 13 historically used morphological characters. Whenever possible type material was examined. The monograph of Stephen and Edmonds (1972) was used as a starting point and changes made in the intervening years are reiterated here. Of the 40 putative species listed in that work or described since then, 12 remain valid species (two moved to other genera), three are reduced to subspecific rank, four are considered either *species inquirendum* or *incertae sedis*, and the remainder (21) are considered junior synonyms. One new monotypic subgenus (*Spinata*) is described. The known distribution of each species is summarized and a key is provided.

This is the last in a series of revisionary articles (begun in Cutler and Murina 1977) addressing those taxa previously treated as subgenera of the sipunculan genus *Golfingia*. Earlier papers dealt with *Mitosiphon*, *Fisherana*, and *Apionsoma* (Cutler 1979), *Golfingiella* and *Siphonoides* (Cutler, Cutler and Gibbs 1983), *Thysanocardia* (Gibbs, Cutler and Cutler 1983), and *Nephasoma* = *Phascoloides* (Cutler and Cutler 1986). The starting point for this paper is the monograph of Stephen and Edmonds (1972) and includes all 35 names listed as valid species in that work, one from another genus, plus the four named since that time. Table 1 lists those names and their current status.

This taxon traces its origins back to an "outing on the greens" of 19th century St. Andrews, Scotland: "... and I have accordingly ventured to dedicate the new genus of Sipunculid worms indicated by this specimen to the local goddess whose cult is historically associated with the most ancient of Scottish seats of learning" (Lanckester 1885:469). There was subsequent confusion about the proper use of this name and the generic name *Phascolosoma* until Fisher clarified the matter in 1950.

Whenever possible we have obtained type

material to verify the original descriptions. In several cases we have made detailed observations on series of recently collected individuals to evaluate better the traditionally used morphological characters. Much of the material for this analysis of variation within populations came from collections near the Kerguelen Islands.

We first discuss the morphological characters in light of our recent analyses. This is followed by a section where each of the species we consider to be valid is discussed; this includes a synonymy and discussion of newly added junior synonyms. The two species previously transferred to other genera and the four species considered to be *incertae sedis* or *species inquirendum* are discussed separately. A key to all the valid species and a summary of their distribution is presented.

The following abbreviations are used in this text for the museums from which we borrowed material: Australian Museum, South Sydney (AMSS); British Museum (Natural History) (BMNH); Irish National Museum, Dublin (INMD); Muséum National d'Histoire Naturelle, Paris (MNHN); Museum für Naturkunde der Humboldt-Universität zu Berlin (MNHU); Musée

Table 1.—Original and proposed names of species of *Golfingia*.

Original name	Proposed name
<i>Golfingia anderssoni</i> (Théel, 1911)	no change
<i>Golfingia anguinea</i> (Sluiter, 1902)	species inquirendum
<i>Golfingia appendiculata</i> (Sato, 1934)	<i>Golfingia muricaudata</i>
<i>Golfingia birsteini</i> Murina, 1973	no change
<i>Golfingia cantabriensis</i> Edmonds, 1960	<i>Golfingia margaritacea</i>
<i>Golfingia capensis</i> (Teuscher, 1874)	no change
<i>Golfingia charcoti</i> (Hérubel, 1906)	<i>Golfingia elongata</i>
<i>Golfingia cylindrata</i> (Keferstein, 1865)	<i>Golfingia elongata</i>
<i>Golfingia derjugini</i> (Gadd, 1911)	<i>Golfingia elongata</i>
<i>Golfingia elongata</i> (Keferstein, 1863)	no change
<i>Golfingia glossipapillosa</i> (Sato, 1934)	<i>Golfingia margaritacea</i>
<i>Golfingia herdmani</i> (Shipley, 1903)	<i>Golfingia vulgaris herdmani</i>
<i>Golfingia hudsoniana</i> (Chamberlin, 1920)	<i>Golfingia muricaudata</i>
<i>Golfingia ikedai</i> Fisher, 1950	<i>Golfingia margaritacea</i>
<i>Golfingia iniqua</i> (Sluiter, 1912)	no change
<i>Golfingia kolensis</i> (Gadd, 1911)	<i>Golfingia vulgaris</i>
<i>Golfingia lagensis</i> (Fischer, 1895)	incertae sedis
<i>Golfingia liochros</i> Cutler & Cutler, 1979	<i>Golfingia vulgaris herdmani</i>
<i>Golfingia margaritacea</i> (Sars, 1851)	no change
<i>Golfingia mawsoni</i> (Benham, 1922)	<i>Golfingia margaritacea ohlini</i>
<i>Golfingia mirabilis</i> Murina, 1969	no change
<i>Golfingia muricaudata</i> (Southern, 1913)	no change
<i>Golfingia mutabilis</i> (Southern, 1913)	<i>Golfingia iniqua</i>
<i>Golfingia nordenskjoldi</i> (Théel, 1911)	<i>Golfingia margaritacea</i>
<i>Golfingia nota</i> (Sato, 1934)	<i>Golfingia margaritacea</i>
<i>Golfingia ohlini</i> (Théel, 1911)	<i>Golfingia margaritacea ohlini</i>
<i>Golfingia okinoseana</i> (Ikeda, 1904)	<i>Golfingia margaritacea</i>
<i>Golfingia owstoni</i> (Ikeda, 1904)	<i>Golfingia vulgaris</i>
<i>Golfingia pectinatoidea</i> Cutler & Cutler, 1979	<i>G. (Spinata) pectinatoides</i>
<i>Golfingia profunda</i> (Roule, 1898)	<i>Golfingia margaritacea</i>
<i>Golfingia pudica</i> (Selenka, 1885) (partim)	<i>Golfingia margaritacea ohlini</i>
<i>Golfingia recondita</i> (Sluiter, 1900)	<i>Apionsoma recondita</i>
<i>Golfingia reticulata</i> (Hérubel, 1925)	incertae sedis
<i>Golfingia rugosa</i> (Southern, 1913)	<i>Golfingia iniqua</i>
<i>Golfingia scutiger</i> (Roule, 1906)	incertae sedis
<i>Golfingia signa</i> (Sato, 1934)	<i>Golfingia margaritacea</i>
<i>Golfingia solitaria</i> (Sluiter, 1912)	<i>Golfingia vulgaris</i>
<i>Golfingia soya</i> (Sato, 1934)	<i>Golfingia margaritacea</i>
<i>Golfingia trichocephala</i> (Sluiter, 1902)	<i>Apionsoma trichocephala</i>
<i>Golfingia vulgaris</i> (de Blainville, 1827)	no change

Océanographique, Monaco (MOMV); Naturhistoriska Riksmuseet, Stockholm (NHRS); National Museum of Canada, Ottawa (NMCO); National Science Museum, Tokyo (NSMT); Royal Scottish Museum, Edinburgh (RSME); University Museum, Oxford (UMOU); United States National Museum (USNM); Zoologisk Museum, Copenhagen (UZMK); Zoological Institute, Leningrad (ZIAS); Zoological Institute, Tohoku University, Sendai (ZITU); Zoolo-

gisch Museum, Universiteit van Amsterdam (ZMUA); Zoological Museum, Bergen (ZMUB); Zoological Museum, Hamburg (ZMUH).

Morphological Characters

The following section includes comments on those features which have historically been used by systematists to describe and differentiate species within this genus. These

descriptions were legitimate attempts but not always based on a good understanding of possible variation within a population (species). These characters are the same as those used in *Nephasoma*. In Cutler and Cutler (1986) parallel observations are presented for that genus. There are striking parallels between these two genera and obvious "species pairs" exist. For example, there is one species in each genus with large bulbous inflated papillae and distinct tails on the posterior end of the trunk (*G. anderssoni* and *N. flagriferum*) and one species in each with hooks in rings (*G. elongata* and *N. rimicola*). *Golfingia margaritacea* and *N. eremita* are twins except for the lack of dorsal retractors in the latter.

1. *Introvert hooks*.—Several species are known to have deciduous hooks and we suspect this is true for most species. Those few putative species reported as lacking hooks are based on individuals over 10 mm long and hooks may have been present in earlier ontogenetic stages. The only "hookless" species remaining after this work is *G. anderssoni* for which the smallest animal recorded to date has a 25 mm trunk. Most species in the genus have small (20–40 μm), scattered, pale hooks. Two species have large (150–300 μm), slender, spinelike hooks (*G. birsteini* and *G. mirabilis*). Between these two extremes are *G. muricaudata* (50–150 μm in small worms) and *G. vulgaris* with dark hooks generally 50–120 μm tall (Saiz-Salinas 1986 reported 20–275 μm hooks and Edmonds 1956 reported 120–200 μm hooks in his var. *queenslandensis* = *G. vulgaris herdmani*).

Two species that have hooks in rings are *G. elongata* (45–100 μm) and *G. (Spinata) pectinatoides* (25–30 μm). These latter ones are unique as they have a small comb of basal spinelets like several of the *Apionsoma* species.

2. *Tentacles*.—The standard pattern is a series of digitate circumoral tentacles whose number and complexity increases with age (Fig. 1; see also Théel 1905, pl. 14, figs. 192–195 or Gibbs 1977). Adult specimens com-

monly have 16–40 units but the number may exceed this in large worms (over 10 cm). The array in *G. nordenskjoldi* was alleged to consist of only two tentacles but what was seen is only the tips of the two larger, dorsal tentacles in an incompletely expanded specimen of *G. margaritacea*. A few species have been reported to have fewer than 16 but most of these were based on small individuals and may not be meaningful. *Golfingia birsteini* with 8–10 very short ones may be one real exception. The tentacular crown in *G. (Spinata) pectinatoides* may be unique, being neither the standard array nor nuchal tentacles. The small diameter and partially retracted state of the specimens precludes a definitive statement.

3. *Caudal appendage*.—The posterior end of the trunk in most species comes to a blunt, rounded terminus but may form a "pencil point" due to contraction of the circular muscle layer (Fig. 2). There are two species (*G. anderssoni* and *G. muricaudata*) which do exhibit a distinct caudal appendage (tail) of variable length being rudimentary in small individuals. This can be a useful character unless the worm is damaged or less than 5 mm long when its apparent absence could be misleading.

4. *Trunk length to width ratio*.—Most species have cylindrical trunks with the length exceeding the diameter by 5–10 times. Since these are very elastic muscular sacs, selective contraction and relaxation of muscle layers can greatly modify these proportions in a single individual and therefore these measurements should not be used in a precise or strict way. There is only one species which is very elongate—*G. birsteini* has a trunk 15–20 times longer than wide. *Golfingia elongata* has been reported as having similar proportions but most individuals are less elongate. One species is consistently at the other end of the spectrum—*G. iniqua* almost always has a length only about three times the diameter, i.e., plump and stout.

5. *Introvert length*.—This measurement is

usually presented as a proportion of the trunk length and there are three problems here: A. As has been demonstrated in other genera the relative length of these two body parts changes with age, the introvert being a larger part of the whole in younger animals and appearing to decrease in relative size due to allometric growth. B. The second problem results from the very plastic form of these animals and extreme elasticity of the introvert in particular. When the introvert is measured in the withdrawn condition the value obtained will be much shorter than in the same worm with a fully extended introvert. C. The third problem results from different ways of determining where the introvert/trunk junction is, i.e., where does the introvert start? We have defined this as being just anterior to the nephridiopores (or anus in those taxa where this is anterior). With this understanding it can be asserted that most species have introverts 0.7–1 times the trunk length. *Golfingia (Spinata) pectinatooides* has a significantly longer one (up to 2×). One other apparent anomaly is in *G. rugosa = iniqua*. The worm Southern (1913) described was 5 mm long: “The proboscis is invaginated for a distance of 2 mm, and its total length from the anus to the tentacular crown is 8.5 mm.” This was changed in Stephen and Edmonds (1972: 107) to read “Introvert up to about 10.5 mm . . .” This could be read as having an introvert twice the trunk length but in Southern’s one worm it should read 1.7× and, more importantly note the small trunk size which reaffirms point A above. Another confusing situation occurs with *G. muricaudata*. Southern (1913) gives measurements which include total length (introvert, trunk and tail) and says that there is “thus considerable variation in the relative proportions.” If one discounts the tail, since it is not part of the trunk but only an appendage, the introvert lengths range from 62–89% of the trunk length. Sato’s (1934) data were misinterpreted by Stephen and Edmonds (1972:109) to suggest a short intro-

vert (less than 50%) in *G. soya*. Some of his measurements are of incompletely extended introverts and the actual range is 65–75%. In summary, except for *G. (Spinata) pectinatooides*, the introvert is from 65–100% of the trunk length in *Golfingia* species and is not a useful character for differentiating species.

6. *Anus/nephridiopores relationship*.—In this genus the anus is either at the same anterior/posterior level of the nephridiopores or slightly posterior to them. In the latter case the distance is rarely more than 1–2 mm in larger worms.

7. *Papillae distribution/size/shape*.—The epidermis of sipunculans has a variety of glandular bodies capable of producing mucus and other products. The number and density of these structures, the degree to which these protrude above the surface to form papillae and the particular shape of these papillae is extremely variable. In almost all species these are more numerous in the anterior and posterior 10–20% of the trunk. These are especially distinct in *G. vulgaris* and large on the posterior end of *G. anderssoni*, but aside from these exceptions, the specificity of form and size ascribed to various species by earlier authors is misleading. Our observations suggest that the age (older worms have larger papillae), microhabitat (a close-fitting hard dwelling stimulates larger papillae) and postmortem chemical history of the worm (bleaching of pigment) has a significant impact on the morphology of these papillae.

8. *Shields*.—This term has caused some confusion within this phylum. The Aspidosiphonidae have a hardened epidermal structure (calcium carbonate or scleroprotein) at the anterior end of the trunk (sometimes posterior also) which is called a shield. This same term has been used to describe a different situation in this genus, i.e., an aggregation of close-packed papillae around the ends of the trunk giving it a dark, rugose appearance as in *G. vulgaris* and its subspecies (Edmonds 1980:19). This is not a shield

as the term is used in the Aspinosiphonidae and its use here should be avoided. A recent example of the problem is in Murina's (1969: 1732) description of *G. mirabilis* where she said "At both ends of the trunk papillae are distributed thickly enough and resemble a shield." Murina (1975) also used this term when creating her new subgenus *Dushana* (see below).

9. *Spindle muscle*.—In most sipunculans there is a thin thread-like muscle running through the gut coil and connecting to it at intervals. The origin of this muscle is either on the body wall anterior to the anus (as in *G. (Spinata)*), or from the wall of the rectum, wing muscle or a small flap of tissue just under it (as in *Golfingia (Golfingia)*). This muscle terminates posteriorly within the gut coil in this genus. In some other genera it extends out of the coil and attaches to the posterior end of the trunk. Whether this muscle is described as strong or weak can be a semantic issue depending on that author's experience and frame of reference. While it may not be equally developed, all *Golfingia* species do have one.

10. *Retractor muscles' point of origin*.—The two pairs of muscles which insert behind the 'head' and function to retract the introvert have their origins on the inner surface of the trunk wall. The position of these attachments along the anterior/posterior axis has been assumed to be meaningful by many authors (Benham 1922 is one exception). Our data from *Nephasoma* suggest that the relative position does change during growth, resulting in an apparent antieriad shift in the point of origin (Cutler and Cutler 1986). The data from this genus are less clear, perhaps because of fewer large worms. The most common condition is for the ventral pair to have its origin in the middle third (35–65% of the distance to the posterior end) and the dorsal pair more anteriorly (10–20%). Two apparent exceptions to this may be in some large *G. muricaudata* or the long, slender *G. birsteini* in which the *ventrals* are around 20%. The other exceptions to this rule are

in *G. mirabilis* and *G. (Spinata) pectinatoides* where the dorsal origins are posterior to the ventrals, both in the anterior quarter.

11. *Intestinal coiling*.—As in other genera the number of gut coils increases with age and is not species specific. This number is commonly 20–30 but the reported range is from 10 to 90. Most species exhibits a tightly wound double helix but this can be disrupted and appear loose.

12. *Intestinal fixing muscles*.—The number of fine, thread-like muscles attaching the gut coil to the body wall varies from 0–4 according to published accounts. This has been alleged to be a species-specific character but our experience suggests that these are very fragile structures and can be easily broken, overlooked, and even if present not mentioned by certain authors. The number of muscles within one population also varies (our *G. margaritacea ohlini*, and Gibbs 1973:81 on *G. elongata*). The one species which appears to lack these is *G. (Spinata) pectinatoides*.

13. *Rectal caecum*.—As in *Nephasoma* this character is difficult to see in small individuals and not consistently present. Also, some authors simply do not mention whether or not it is present but this should not be interpreted as equivalent to being absent.

Summary.—Of these 13 characters six have some usefulness to the systematist (1, 2, 3, 4, 7, 10) while the remaining seven do not help differentiate species within *Golfingia (Golfingia)*. We have been unable to discern any helpful new morphological characters.

Systematic Section

Genus *Golfingia*, Lankester, 1885

Type species.—*Sipunculus vulgaris* (de Blainville, 1827).

Diagnosis.—Species small to large sized; body wall with continuous muscle layers; oral disc carries tentacles arranged around mouth; four introvert retractor muscles;

contractile vessel without true villi; spindle muscle not attached posteriorly; two nephridia.

Key to *Golfingia* Species

1. Nephridia bilobed, both pair of retractors close to ventral nerve cord, hooks with basal spinelets, spindle muscle anterior to anus
..... *G. (Spinata) pectinatoides*
- Nephridia unilobed, anterior retractors dorso-laterally displaced, hooks (if present) without basal spinelets, spindle muscle posterior to anus or on rectum subgenus *Golfingia* s.s. 2
2. Caudal appendage present 3
- Caudal appendage not present ... 4
3. Large bladderlike papillae at base of caudal appendage *G. anderssoni*
- Base of caudal appendage without large bladderlike papillae
..... *G. muricaudata*
4. Introvert hooks in rings .. *G. elongata*
- Introvert hooks scattered, if present 5
5. Anterior and posterior ends of trunk dark and coarsely papillated 6
- Ends of trunk not distinctly different color/texture 7
6. Ventral retractor muscles originate posterior to dorsal pair *G. vulgaris*
- Ventral retractor muscles originate anterior to dorsal pair *G. mirabilis*
7. Trunk length less than 3 times the width *G. iniqua*
- Trunk length more than 3 times the width 8
8. Reduced tentacles, large hooks (>150 μm) *G. birsteini*
- Normal tentacles, hooks, if present, small (<75 μm) 9
9. Contractile vessel simple, without bulbous swellings *G. margaritacea*
- Contractile vessel with bulbous swellings/vesicles, often orange colored, southern Africa *G. capensis*

Golfingia (Spinata), new subgenus

Type species. — *Golfingia pectinatoides* Cutler and Cutler, 1979.

Diagnosis. — Small to medium sized with introvert longer than trunk; small hooks with basal spinelets and arranged in rings; slender retractor muscles about equal in size and both pairs very close to ventral nerve cord; spindle muscle originates from the body wall just anterior to anus; nephridia bilobed.

Remarks. — This monotypic subgenus is an inhabitant of shallow warm waters. There is a suite of character states (retractors, hooks and nephridia) which this taxon shares with *Phascolosoma (Edmondsius) pectinata* and several *Apionsoma* species. This is most likely an example of convergent or parallel evolution. The decision to place this taxon in *Golfingia* is based on the arrangement of the tentacles which appear to be around the mouth (no individual has its introvert completely extended) and the spindle muscle not inserted posteriorly on the body wall. There is real need for closer analysis of these similar species using non-morphological characters. The subgeneric name refers to the presence of small basal spinelets on the hooks.

Golfingia pectinatoides Cutler and Cutler, 1979

Golfingia pectinatoides Cutler and Cutler, 1979a:951–954, figs. 3–5.

Material examined. — Type material: MNHN and USNM.

This inhabitant of coral reefs is distinctive. The important characters are those of the subgenus. Additionally, the gut is in an irregular loose coil and there are no fixing muscles.

Known distribution. — Coral reefs at Tulear, Madagascar, and Moorea Island, French Polynesia, at intertidal depths.

Subgenus *Golfingia* (sensu stricto)
Lankester, 1885

Type species.—*Sipunculus vulgaris* (de Blainville, 1827).

Diagnosis.—Introvert equal to or shorter than trunk; simple hooks usually scattered if present (rings in *G. elongata*); anterior pair of retractor muscles with origins more dorsally placed than posterior ventral pair; spindle muscle originates from wall of rectum (sometimes under wing muscle); nephridia unilobed.

We first present a consideration of the most complex “superspecies” in this genus which will be followed by the remaining valid species in alphabetical order.

Comments on the “*margaritacea*” Section

As seems to be true in several genera there is here one very widespread and ill defined species (superspecies?) which has a long and complex history. This morph has retained most of those characters thought to be plesiomorphic (Cutler and Gibbs 1985) with no distinguishing traits other than the lack of anything unique. We here present a summary of those names which have been considered to be some kind of subset of *G. margaritacea* by previous authors. In a later section we propose additional changes.

Sars introduced the name *Sipunculus margaritaceus* in 1851. It consisted of four sentences in Norwegian, had no illustrations and was based on an unspecified number of individuals from Norwegian fjords. This was summarized in Latin in the same year by Diesing as a five phrase description.

In 1865 Keferstein introduced *Phascolosoma oerstedii* from Greenland, and Quatrefages used *Siponcle oerstedii* referring to Keferstein’s material; this genus name was not used by subsequent authors. Koren and Danielssen (1875) treated *oerstedii* as a junior synonym of *G. margaritacea*. However, Théel (1875) and Horst (1882) continued to treat it a a species. Selenka et al.

(1883) and J. Fischer (1914) both considered it to be a junior synonym.

The name *Phascolosoma capsiforme* was put forth by Baird in 1868 for some Falkland Island worms. Théel (1911) reduced this to be a junior synonym. It was continued as a variety by Fischer (1913) who in 1920 reconsidered and also treated it as a junior synonym. However, Leroy (1936) ignored them and listed it as a species. In 1965 Edmonds used it at the subspecific rank, but in Stephen and Edmonds (1972), it again was reduced to a junior synonym.

The next names appeared in 1875: *Phascolosoma albidum* and *P. fulgens* by Théel for far North Atlantic material. Selenka et al. (1883) and J. Fischer (1914) both reduced these names to junior synonyms.

In 1881 Danielssen and Koren named *Stephanostoma hanseni* for some Norwegian arctic worms. This was changed to *Phascolosoma hanseni* by Selenka et al. (1883). Théel (1905) first synonymized *Stephanostoma barentsei* (Horst, 1882) with *P. hanseni* and then divided this taxon into two “forms”: *occidentalis* and *orientalis*. Sluiter (1912) used this name for one specimen. Fischer (1922a and 1924) considered this whole complex to be synonymous with *G. margaritacea*. In 1925 Wesenberg-Lund used *P. hanseni* as a species. Stephen (1941), Wesenberg-Lund (1955), and Stephen and Edmonds (1972) used it as a subspecies. In 1974, Gibbs demoted it again to the status of a junior synonym, and we concur.

Michaelsen in 1889, introduced three names for several Antarctic specimens: *Phascolosoma georgianum*, *P. fuscum*, and *P. antarcticum*. These names were repeated by Fischer (1895) and Hérubel used one in 1906 and another in 1908. In 1911, Théel synonymized all three names under *G. margaritacea*, and we concur. But, *antarcticum* has continued to appear as a subspecies or varietal name up to the present.

The next new name, *Phascolosoma japonicum*, was introduced by Ikeda in 1904

for Japanese material. In 1947, Chin mistakenly applied this name to something with only one pair of retractor muscles. Fisher (1950) changed this name to *Golfingia ike-dai* (since *P. japonicum* was unavailable; see *P. japonicum* Grube). Cutler and Cutler (1981) reduced this to the rank of subspecies.

In 1905 Théel named *Phascolosoma trybomi* from Sweden, but in 1924 Fischer suggested that it should be treated as a variety of *G. margaritacea* and this was also the conclusion arrived at by Lindroth (1941). However, Stephen (1934) used it as a species and then (1941, 1948, 1960) treated it as a subspecies. This last choice was also followed by Wesenberg-Lund (1955), Murina (1957), and Stephen and Edmonds (1972). We do not concur but treat it as a junior synonym.

In the same year, Théel (1905) split the species into two forms, "siberica" and "finmarchica." These were transformed to subspecies in Stephen and Edmonds (1972). Gibbs (1974) asserted that "finmarchica" must be considered synonymous with the nominate subspecies. We treat both names as junior synonyms.

Roule (1906) erected the taxon *Phascolosoma profundum* off the Azores, but this name went unused until Stephen and Edmonds (1972). In 1977 Cutler and Murina placed it in the synonymy of *G. margaritacea*.

In 1908 Lanchester named *Phascolosoma socium* for Antarctic material which Fischer (1929) submerged as a junior synonym.

Sluiter (1912) introduced *Phascolosoma iniquum* from the NE Atlantic which also went unused until Stephen and Edmonds (1972). Cutler and Murina (1977) reduced this to the status of a junior synonym. Gibbs (1986) considered this a valid species and a senior synonym of *G. mutabilis* and *G. rugosa*.

In the same year, Sluiter (1912) erected *Phascolosoma pusillum* from the Cape Verde Islands. Wesenberg-Lund (1959a:209) "is

inclined to regard" it as a junior synonym, but Stephen and Edmonds (1972) transferred the taxon to the subgenus *Golfingiella* and made no reference to Wesenberg-Lund's paper. In 1977 Cutler and Murina considered this entity to be a junior synonym of *Golfingia (Mitosiphon) trichocephala* (now *Apionsoma trichocephala* sensu Cutler 1979).

Gerould (1913) created the subspecies *Phascolosoma margaritacea meridionalis* for a population off North America. This was repeated in Stephen and Edmonds (1972), but the name has not been applied to any new material (see Cutler 1973). It was differentiated from the nominate form by being very elongate (length often 10–20 times the width). Its biological significance is doubtful.

In 1934 Sato named *Phascolosoma noto* and *P. soyo* from the Sea of Japan; they were not mentioned again until Stephen and Edmonds (1972). In Cutler and Cutler (1981) *G. soyo* was demoted to a subspecies with *G. noto* its junior synonym.

Fisher (1952) erected a subspecies, *Golfingia margaritacea californiensis*, which was maintained by Stephen and Edmonds (1972), Gibbs (1974), and Rice (1980) based only on Fisher's original material. The assertion that this form deserves subspecific rank is based on tentacle number and morphology, skin thickness/roughness and number of fixing muscles. As discussed in the Introduction these characters are too variable to be used in this way.

Four years later Edmonds (1956) established *Golfingia margaritacea adelaidensis* from Australia which was repeated in Stephen and Edmonds (1972) and Edmonds (1980). Murina (1977:230) listed it in the synonymy of *G. margaritacea margaritacea*. This subspecies has only been reported from Southern Australia but in many ways resembles both the shallow water *G. margaritacea* from Japan and the South African *G. capense*. This is only known from large (60–100 mm trunk) shallow water speci-

mens. It supposedly differs from the nominate form on such characters as strength and attachment of spindle muscle, number of fixing muscles, color, and a more rudimentary caecum. While this may be a biologically distinct taxon our anatomical analysis makes the retention of this subspecific rank difficult to justify. Future analyses of this population should consider the possibility of a shallow water Indo-West Pacific taxon with a strong spindle muscle attaching under the wing muscle and a voluminous contractile vessel.

Edmonds (1960) also named a new species from New Zealand, *Golfingia cantabriensis*, which was later (Cutler and Murina 1977) synonymized with *G. margaritacea*.

Summary.—The reason that so many names have been used for a single species rests largely in the variability of the external form. The characters used by these authors to differentiate the taxa have included: overall size (few to several hundred millimeters long); color (e.g., yellowish to reddish brown, dirty pink, bluish white, straw, rust and the following shades of grey: reddish, whitish, brownish, yellowish, or bluish); ratio of introvert to trunk length (up to 1.2:1), thickness/texture of skin (thin to thick, smooth to corky, translucent to opaque, with or without reticulations); papillae shape, size, and distribution; shape of the posterior end (with or without “tail”); and the presence and distribution of introvert hooks. Perhaps the most elaborately described external feature has been the tentacular crown (from few to many tentacles). The relative position of the nephridiopore and anus has also been utilized by some authors.

The internal anatomy has been used but to a lesser extent, e.g., the number of gut coils (but without reference to the size of the individuals), the number of fixing muscles, and presence of a rectal caecum. As noted above many of these characters do vary with size of the worms, nature of the microhabitat, or the preservation methods.

Some of these biologists had limited ex-

perience with both the worms and the sipunculan literature. Also, they were working within the paradigm of a typological species concept. The kind of analysis we have engaged in suggests to us that these variations are all possible within one biological species but willingly acknowledge that we could be wrong and hope that different kinds of data can be generated to test this hypothesis.

Golfingia margaritacea margaritacea
(Sars, 1851)

In Stephen and Edmonds (1972:94) there is a lengthy synonymy for this species and those taxa considered subspecies at that time, which we will not repeat here. What follows is only a partial synonymy including the original author and changes made since 1970.

Sipunculus margaritaceus Sars, 1851:196–197.

Golfingia margaritacea.—Murina, 1971:42; 1972:301; 1973:69; 1974:235; 1977:230–232; 1978:122.—Cutler, 1973:136–138; 1977a:139–140.—Gibbs, 1974:871–876; 1977:12–13.—Cutler and Murina, 1977:176–177.—Cutler and Cutler, 1979b:104; 1980b:197–198.—Frank, 1983:12–13.—Cutler, Cutler and Nishikawa, 1984:263–264.—Saiz-Salinas, 1984:180–182; 1986:21–22.

**Golfingia margaritacea adelaidensis* Edmonds, 1956:302–303, pl. 2, fig. 2; 1980:21.—Stephen and Edmonds, 1972:97.—Murina, 1977:230.

**Golfingia margaritaceum californiense* Fisher, 1952:392–393.—Stephen and Edmonds, 1972:97–98.—Rice, 1980:494.

Phascolosoma margaritacea finmarchica Théel, 1905:63–64.

**Golfingia margaritacea finmarchica.*—Stephen and Edmonds, 1972:98.

Phascolosoma margaritaceum forma sibirica Théel, 1905:64–65.

**Golfingia margaritacea sibirica.*—Stephen and Edmonds, 1972:99.

- Phascolosoma antarcticum* Michaelsen, 1889:73–84.
- Phascolosoma margaritaceum* var. *antarcticum*.—Fischer, 1929:481.
- **Golfingia margaritacea antarctica*.—Stephen and Edmonds, 1972:97.—Cutler, Cutler and Nishikawa, 1984:265.
- Golfingia cantabriensis* Edmonds, 1960:163–164, text-fig. 4.—Stephen and Edmonds, 1972:86–87.
- Phascolosoma glossipapillosum* Sato, 1934:10–12, pl. 1, fig. 5.
- Golfingia glossipapillosa*.—Stephen and Edmonds, 1972:91.—Murina, 1977:229.—Cutler and Cutler, 1981:61–62.
- Phascolosoma hansenii* Danielssen and Koren, 1881:9–13.
- Phascolosoma margaritaceum hansenii*.—Stephen, 1941:253.
- **Golfingia margaritacea hansenii*.—Wesenberg-Lund, 1955:9.
- Phascolosoma japonicum* Ikeda, 1904:5–7, figs. 2, 28, 29.—Chin, 1947:100.
- Golfingia ikedai*.—Fisher (nom. nov. pro *Phascolosoma japonicum* Ikeda, 1904, non *Physcosoma japonicum* Grube, 1877), 1950:550; 1952:390.—Stephen and Edmonds, 1972:92.—Murina, 1977:228–229.—Nishikawa, 1977:11.
- Golfingia margaritacea ikedai*.—Cutler and Cutler, 1981:63.—Cutler, Cutler and Nishikawa, 1984:264–265.
- **Phascolosoma margaritaceum* var. *meridionalis* Gerould, 1913:382.
- Golfingia margaritacea meridionalis*.—Stephen and Edmonds, 1972:98–99.
- Golfingia mawsoni*.—sensu Murina, 1964:230–233.
- Phascolosoma nordenskjoldi* Théel, 1911:30–31, pl. 3, figs. 35–41.—Fischer, 1920:416; 1922b:34; 1929:483.—Stephen, 1941:253–254; 1948:217.
- Golfingia nordenskjoldi*.—Wesenberg-Lund, 1955:9–11.—Murina, 1964:237–238; 1978:122.
- Phascolosoma noto* Sato, 1934:14–16, pl. 1, fig. 7, text-fig. 17.
- Golfingia nota*.—Stephen and Edmonds, 1972:102.—Murina, 1977:234.—Cutler and Cutler, 1981:63.
- Phascolosoma okinoseanum* Ikeda, 1904:9–12, text-figs. 4, 34–38.
- Golfingia okinoseana*.—Stephen and Edmonds, 1972:103.—Murina, 1977:223.—Cutler and Cutler, 1981:64.—Cutler, Cutler, and Nishikawa, 1984:263.
- Phascolosoma profundum* Roule, 1898:385; 1906:74–77.
- Golfingia profunda*.—Stephen and Edmonds, 1972:104.—Cutler and Murina, 1977:176–177.
- Phascolosoma signum* Sato, 1934:16–17, pl. 1, fig. 8, text-fig. 18.
- Golfingia signa*.—Stephen and Edmonds, 1972:108.—Murina, 1977:233.—Cutler and Cutler, 1981:65.—Cutler, Cutler and Nishikawa, 1984:266.
- Phascolosoma soyo* Sato, 1934:17–20, fig. 9, text-figs. 19–21.
- Golfingia soya*.—Stephen and Edmonds, 1972:109.—Murina, 1977:233–234.
- Golfingia margaritacea soyo*.—Cutler and Cutler, 1981:66.—Cutler, Cutler and Nishikawa, 1984:265.
- Phascolosoma trybomi* Théel, 1905:69–70.
- Phascolosoma margaritaceum trybomi*.—Fischer, 1924:72.
- **Golfingia margaritacea trybomi*.—Wesenberg-Lund, 1955:8.—Murina, 1971:42; 1977:232–233.

Material examined.—Types: AMSS, *G. margaritacea adelaidensis* Edmonds; BMNH, *P. capsiforme* Baird; NHRS, *P. nordenskjoldi* Théel; USNM, *G. margaritaceum californiensis* Fisher and *G. m. meridionalis* Gerould; ZITU, *P. soyo* Sato; ZMUB, *P. hansenii* Danielssen and Koren; ZMUH, Michaelsen's three species, *P. antarcticum*, *P. fuscum*, *P. georgianum*; ZMUT, *P. japonicum* Ikeda (= *G. ikedai*). Also: recently collected specimens of *G. ikedai* from near the type locality; *G. soya* from the Japan Sea (*G. nota* cannot be located); some *G. margaritacea* from the East Atlantic Ocean at UZMK and NHRS identified by

Wesenberg-Lund, and at NHRS some identified by Théel.

There are eight names used as subspecies in Stephen and Edmonds (1972) which we regard as undeserving of that rank/status. These are marked with an * in the above synonymy and are discussed in the preceding, "Comments on the '*margaritacea*' Section." The following nine names were presented as valid species in Stephen and Edmonds (1972). We conclude that these should be treated as junior synonyms of *G. margaritacea*. Following that is the single taxon we present as a subspecies.

Cutler and Murina (1977) reduced *G. cantabriensis* to the status of a junior synonym. Subsequent analysis of the single specimen showed it to be in very poor condition and complete examination is prohibited. There are only some subtle external differences.

Golfingia glossipapillosa was discussed in Cutler and Cutler (1981) where they raised questions about its biological validity but did not change its status. However, in Cutler, Cutler, and Nishikawa (1984) this was reduced to the status of a junior synonym.

Cutler and Cutler (1981) determined *G. ikedai* to be a subspecies of *G. margaritacea*. The putative difference at that time was the bulbous and vesicular contractile vessel in larger worms. In Cutler, Cutler, and Nishikawa (1984) it was noted that some individuals from a particular population (trunks less than 20 mm) bore scattered small hooks. It is now apparent that these differences are not unique.

Golfingia okinoseana was discussed in Cutler and Cutler (1981), and at that time it was left unchanged despite a very weak foundation (one specimen). Cutler, Cutler, and Nishikawa (1984), after finding no new material in their collections of over 3200 worms, reduced this to a junior synonym.

Cutler and Cutler (1981) determined *G. nota* and *G. soya* to be conspecific and reduced this combined taxon to subspecific rank. They did not consider it conspecific

with the nominate form based on the large, cone- or pear-shaped papillae on the proximal portion of the introvert. This is not a clear distinction, and since no additional specimens have been located for comparative studies, we now further reduce the rank of this taxon.

The type material of *G. nordenskjoldi* at NHRS consists of three vials. No. 218 has only an introvert with many tentacles. No. 219 has three specimens, one of which is missing its introvert. No. 220 has three specimens, the largest has a 5 mm trunk which is rough. One does appear to have only two tentacles, but the introvert is not completely extended. Fischer did not have new material but merely repeated Théel's record. It is now clear that these worms are merely a few young animals.

Golfingia profunda was determined to be a junior synonym in Cutler and Murina (1977).

Golfingia signa (Sato 1934) was discussed in Cutler and Cutler (1981). Cutler, Cutler, and Nishikawa (1984) concurred by retaining the name but expressed reservations. Its putative differences from *G. margaritacea* are only external, mostly the wavy, zig-zag ridges on the posterior end of the body. We have found this condition in other material from different parts of the world and we can no longer justify specific rank for this name.

The variations in the morphology of this taxon have been commented on above. It is therefore a very difficult species to describe with precision. Aside from the generic and subgeneric characters and the above comments on the variations one can add very little.

Known distribution.—*Golfingia margaritacea margaritacea* is a very widely distributed taxon living in all sectors of the Atlantic, Arctic and Antarctic Oceans (80°N–78°S); the North, Southeast and Southwest Pacific (over 30°N and S) with a few exceptions at lower latitudes but in deep water (over 2000 m). The depth range is 1–5300 m but most specimens have been col-



Fig. 1. *Golfingia margaritacea ohlini*, the generalized golfingiid morph: A, Whole animal; B, Tentacular crown. (Scale lines are 2 and 0.5 mm.)

lected from depths less than 300 m. It is unknown from the Indian Ocean and Mediterranean Sea.

Golfingia margaritacea ohlini (Théel, 1911)
Figs. 1, 2

Phascolosoma ohlini Théel, 1911:29–30, pl. 2, figs. 21–23, pl. 3, figs. 24–27, pl. 5, figs. 69–70.—Fischer, 1920:413; 1929:484.—Stephen, 1941:254–255.

Golfingia ohlini.—Wesenberg-Lund, 1955:10; 1963:106–107.—Edmonds, 1965:31.—Stephen and Edmonds, 1972:102.—Murina, 1972:301–302; 1974:235; 1978:122.—Cutler and Cutler, 1980b:199.

Not *Golfingia ohlini*.—Wesenberg-Lund, 1959b:61 (see *G. elongata*).

Phascolosoma mawsoni Benham, 1922:13–17.—Fischer, 1929:482–483.—Stephen, 1948:218.

Golfingia mawsoni.—Edmonds, 1972:84–85.—Murina, 1972:301; 1977:225–227.—Stephen and Edmonds, 1972:99–100. Not Murina, 1964:230–233.

Phascolosoma pudicum Selenka, 1885:11–12.—Fischer, 1929:484.—Stephen, 1948:217–218.

Golfingia pudica.—Stephen and Edmonds, 1972:104–105.—Cutler, Cutler and Gibbs, 1983:671–672.

Golfingia vulgaris [sic] var. *antarctica* Murina, 1957:996–997.

Golfingia vulgaris murinae.—Stephen and Edmonds, 1972:111.

Material examined.—Types: NHRS, *G. ohlini*; AMSS, *G. mawsoni*; additional recently collected specimens from subantarctic waters near the Kerguelen Islands. *G. pudica*: BMNH, Type material; UMOU, one specimen which we believe to be part of the original collection; UZMK, a specimen of Wesenberg-Lund's from Mauritius; ZIAS, a specimen of Murina's from the East China Sea.

The following is a chronologically-arranged, historical review of this taxon.

In 1911 Théel named this species from five specimens collected at 24–95 m off South Georgia. The total body length was 6–17 mm with a pointed posterior extremity having crowded cylindrical papillae. The anus was “in the middle of the body” with the nephridia at the same level; therefore, as currently defined, the trunks were 3–9 mm long with introverts of equal length. There were 10–16 tentacles. He compared these worms to *G. cylindrata* but the hooks and papillae separated them. Our examination of this material showed the following: Vial no. 215 is the very small one which is listed as holotype in Stephen and Edmonds (1972). This worm had never been opened and proved to have only two retractor muscles; therefore it is a *Nephasoma*, not a *Golfingia* species. No. 216 has

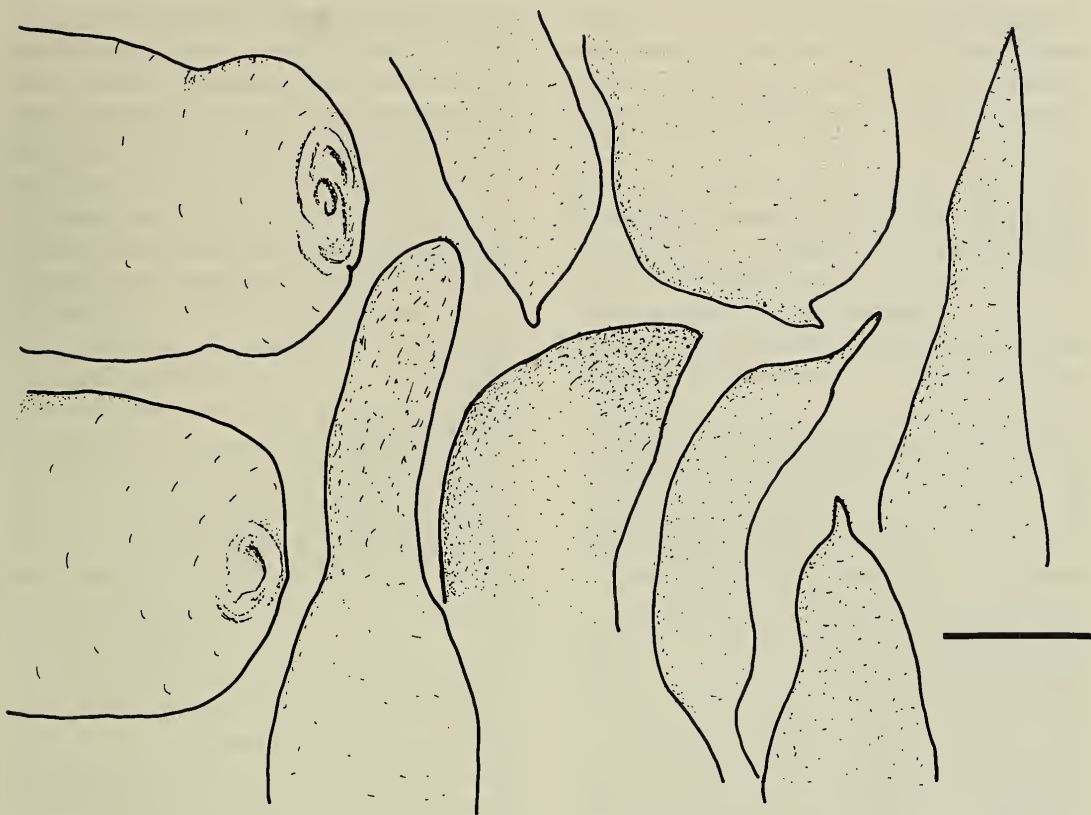


Fig. 2. Posterior ends of some *Golfinigia margaritacea ohlini* from the Kerguelen Islands showing possible variation in form within one population. (Scale line is 1 mm.)

two large worms with eggs in the coelom, a "pencil point" posterior end, and no visible hooks. No. 217 has two worms packed with sperm and has small introvert hooks. These also had never been dissected but do have four retractor muscles. They are very similar to the small Japanese *G. margaritacea* reported by Cutler, Cutler, and Nishikawa (1984).

In 1920 Fischer recorded one *G. ohlini* from 385 m off Australia with hooks and 12 tentacles (therefore a small worm?). He apparently repeated this record in 1929.

When Benham described *G. mawsoni* in 1922 he had 50 worms with total length ranging from 8–42 mm. He had some interesting comments about how one "cannot put much reliance on proportions of length of various regions or upon such features as the exact position of the origin of the intro-

vert retractor muscles." He also discussed how contractions of the circular and longitudinal muscle layers could modify the shape of the posterior end. His assertion that this species was clearly distinct from *G. margaritacea* was less than convincing since he based that distinction on the color and texture of the skin plus the presence of a "distinct cone" at the posterior tip. He also mentioned the "longer introvert" and other unspecified differences. Our examination of the type collection served to confirm the accuracy of his description and figures. Only our conclusions were different. Seven years later Fischer (1929) repeated Benham's record from Commonwealth Bay. He had no new material.

In 1941, Stephen reported 24 *G. ohlini* from the Falklands at 130–720 m. Our examination of this material showed it to agree

well with Théel's animals but not all of them have hooks, they have more tentacles, and come from deeper water. The vial from station WS-33 also contains some *Nephasoma* species.

The next record of *G. mawsoni* was Stephen (1948:218) where he recorded about 200 worms (size not mentioned) from near the type locality at depths of 163–300 m. His one morphological observation of interest was that the posterior cone was hardly ever sunk into a "pit" as many of Benham's were.

In 1955 Wesenberg-Lund reported a single, 8 mm *G. ohlini* from 270 m off Chile. We could not examine the tentacles or hooks, and this could have been almost any member of the genus. Her comment "... rather long, cylindrical papillae crowded at the posterior extremity of the body and characteristic of this species were distinct under the microscope" reflects a dependency on one of the most labile characters.

In 1957 Murina described the new variety *G. vulgaris* var. *antarctica* but on the copy sent to us had drawn a line through that name and written in *G. ohlini* (see 1972).

In 1959b Wesenberg-Lund recorded one *G. ohlini* from intertidal water on Mauritius. Our examination of this worm showed it to be a member of this genus with hooks but with no posterior point. According to Wesenberg-Lund, it has 24 tentacles and 15 rings of hooks with 30 hooks per ring. This habitat makes the record very suspect and, given hooks in rings and slender proportions, this worm should be considered a *G. elongata*.

In 1963 Wesenberg-Lund recorded five specimens of *G. ohlini* from 12–13 m in False Bay, South Africa. These measure 5–19 mm, and the largest one has 30 tentacles. In her discussion of the tentacles and nuchal organ, she has the dorsal and ventral sides reversed. Hooks are present and scattered.

After a gap of sixteen years, *G. mawsoni* was used again by Murina (1964:230–233) where she gave a detailed account of two

specimens from 3990 m in the Bering Sea. These worms had trunks 35 and 40 mm long and introverts shorter than the trunks. She felt these fit Benham's species despite a few differences such as the introvert length and anterior position of the retractor muscles. She accounted for this by ontogenetic changes which she discussed at some length including an interesting quote from Gerould (1913) about these problems. The drastically different depth and far northern latitude of these two worms raises our doubts about these belonging to the same gene pool as the shallow Antarctic populations. Therefore, we have moved these two worms to *G. margaritacea margaritacea*.

In 1965 Edmonds reported five *G. ohlini* from 5–432 m in the Ross Sea. These were 8–22 mm long with introverts a little shorter than the trunks and 14–16 tentacles. Hooks were in irregular rows. He identified these on the bases of size, shape, number of tentacles, retractors, and hooks.

Murina (1972) recorded two smaller *G. mawsoni* from the South Atlantic (South Africa, 318 m and Argentina, 75 m) which seem to fit more closely Benham's species. In this same article, she also has *G. ohlini* with *G. vulgaris* var. *antarctica* as a junior synonym. This latter record was based on 17 specimens from 59–1900 m in the Antarctic Ocean. Their trunks are 3–14 mm and posterior ends range from blunt to pointed with obvious tail-like appendage. This paper also contained *G. margaritacea*.

In that same year, Edmonds (1972) published on a collection of 47 *G. mawsoni* from the Antarctic with introverts shorter than the trunk (maximum length 30 mm, most between 18 and 24 mm) and other "minor" differences from Benham's description. Some had short, sharp pointed posterior ends.

Also in 1972, Stephen and Edmonds differentiate *G. mawsoni* from *G. margaritacea* in their key to this genus by the presence or absence of a rectal caecum, and from *G. nota/soya* by the number of fixing muscles

(3 vs. 2). *Golfingia mawsoni* has not been used since.

In 1974 Murina reported five *G. ohlini* from 932–1435 m off the Falklands. The largest trunk is 3.5 mm, but she said that the color of the body and the form of the papillae allowed her to identify them. This assertion is difficult to accept. She went on to compare it to the “closely related” *G. vulgaris* from which it differs, according to her, by the form of the nuchal organ and posterior papillae.

In 1978 Murina added two *G. ohlini* from 710–850 m south of New Zealand. Then Cutler and Cutler (1980b) recorded 96 specimens of *G. ohlini* from the far South Atlantic at 81–247 m. These were 2.5–12 mm long with hooks 17–90 μm high (most less than 50 μm) and pencil point or nipple-like posterior ends.

In his account of the Australian sipunculans, Edmonds (1980) lists the earlier records of *G. ohlini* but has no new records.

Golfingia pudica was discussed at length in Cutler, Cutler, and Gibbs (1983) wherein it was shown that this name had been used for two different populations, one is an *Apionsoma* species and the other, original of Selenka's, is a *Golfingia* species. Selenka said it differed from *G. vulgaris* in distribution of hooks, number of tentacles, and distribution of papillae. Not all of the type specimens have hooks but in those which do, the arrangement is not in distinct rings as Selenka alleged. Fischer (1929) merely repeated Selenka's record. Stephen's (1948) material was badly damaged and cannot now be located. Both of these collections came from the Kerguelen Islands, a common locality for *G. margaritacea ohlini*.

In summary, this taxon is defined by us as a population whose morphology grades into that of *G. margaritacea* from northern waters. The two alleged differences are the presence of hooks in some of these (see Introduction) and the difference in the shape of the posterior end of the trunk (pointed not round). After examining all the litera-

ture, the type material, and many newly collected specimens, the putative differences fade into a cloud of variation. Hooks are only present in smaller worms, and the form of the posterior end varies widely even within one dredge sample (Fig. 2). The decision to rank this at the subspecific level is based on the assumption that there is significant reduction in gene flow but that it is not completely reproductively isolated.

Known distribution.—It has been collected in Antarctic and subantarctic waters including the southern tips of South America and Africa, several southern islands and Antarctica (most between 44° and 77°S). The depths are commonly less than 300 m with a few as deep as 1425 m.

This particular population is extremely interesting from an evolutionary standpoint since the *G. margaritacea* ‘superspecies’ is closer to the hypothetical ancestral sipunculan than any other extant taxon (has the fewest apomorphic character states, see Cutler and Gibbs 1985). Its distribution in the southern seas places it in an excellent position (i.e., a “center of dispersal”) to serve as an ancestral stock for other cold water taxa as habitats opened up during the Cenozoic (Zinsmeister and Feldmann 1984).

Golfingia anderssoni (Théel, 1911)

Phascolosoma anderssoni Théel, 1911:28–29, pl. 2, figs. 28–34, pl. 5, figs. 71–74.—Fischer, 1929:481.—Stephen, 1941:250–251; 1948:216.

Golfingia anderssoni.—Murina, 1957:992–993; 1964:222–224; 1971:42; 1972:296–298; 1974:234; 1977:222–223.—Edmonds, 1965:30.—Stephen and Edmonds, 1972:84–85.

Material examined.—Types: NHRS, three vials of specimens labeled type, no designated holotype. Also recently collected specimens from the South Atlantic.

This is a well-defined species with a solid foundation having the distinctive posterior trunk papillae and caudal appendage. In

many ways it is very similar to *Nephasoma flagriferum*.

Known distribution.—Eight of the 11 published records are from the far southern latitudes at a depth range of 75–1880 m. One is from the Atlantic Ocean at 17–19°S, 4335–4613 m. There are two records, each of a single specimen, from deep water (3150 and 6135 m) in the northern Pacific Ocean (28° and 44°N). These two northern hemisphere records seem peculiar and additional records would help solidify this pattern.

Golfingia birsteini Murina 1973

Golfingia birsteini Murina, 1973:942–943, fig. 1.—Frank, 1983:10–11.

Material examined.—Type: ZIAS.

This long slender species (length up to 15 times the width) with reduced tentacles is similar to several *Nephasoma* species. The papillae are variable in shape (Murina said ‘pear-shaped’). The posterior end does not bear a caudal appendage but is cone-shaped as the result of circular muscle contraction. The hooks are large and scattered, not in rings, and it has no eyespots; thus, is different than *G. elongata*.

Known distribution.—Only one record (seven worms) from the Northwest Pacific (58°N, 149°W) at 3200 m.

Golfingia capensis (Teuscher, 1874)

Phascolosoma capense Teuscher, 1874:488–489, pl. 19, figs. 4, 5, 12, 14.—Selenka et al., 1883:29–30.—Selenka, 1885:12.—Sluiter, 1898:443.—Fischer, 1895:14; 1920:414; 1922a:9–10; 1922b:16.—Leroy, 1936:425.—Stephen, 1942:251.

Golfingia capensis.—Wesenberg-Lund, 1959c:181–182; 1963:108–110.—Stephen and Cutler, 1969:114–115.—Stephen and Edmonds, 1972:87.—Cutler, 1977a:139.

Dendrostoma stephensoni Stephen, 1942: 252–253, pl. 1, fig. 5.

Dendrostomum stephensoni Wesenberg-Lund, 1963:133–134, fig. 10.

Themiste stephensoni.—Stephen and Cutler, 1969:116.—Stephen and Edmonds, 1972:212–213.—Cutler, 1977b:154.

Material examined.—ZMUH, a worm labeled “type” from Lagos but it had been identified by Fischer so probably was not Teuscher’s material; also four specimens from “the Cape, Africa” but no additional station data. NHRS, one worm identified by Fischer from “Cape, Africa.” UZMK, one very large worm (over 18 cm) from “Koreas Kyst, 110 m” with no indication of who identified it or when and Wesenberg-Lund’s specimens of *Themiste stephensoni*. RSME, type material of *T. stephensoni*.

There is a semantic problem with the term ‘villi’ in this common but localized species. The contractile vessel does have bulbous swellings or vesicles along a portion of its length but these are not villi in the sense of Cutler and Cutler (1982:750). No member of this genus bears true contractile vessel villi. This expanded vessel is similar to that seen in intertidal populations from Japan (*G. margaritacea ikedai* in Cutler and Cutler 1981) and this expanded surface area is probably an adaptation to lower oxygen tension in warmer shallow waters. A few small individuals in both these populations also bear small hooks.

This species shares many characters with *G. margaritacea*, especially the shallow water Australian and Japanese populations with bulbous contractile vessels. If it is truly reproductively isolated (i.e., not an Indo-West Pacific taxon) it must differ at only a few loci. Whether one interprets the large size of some members of this population (up to 20 cm) as under genetic control or simply epigenetic plasticity is important. Given our present knowledge we cannot answer several important questions, so will, at this time, not reduce this to the status of a subspecies of *G. margaritacea*.

When we reexamined the *Themiste ste-*

phensoni material it became clear that these worms actually belonged to *G. capensis* (Gibbs and Cutler, 1987). The putative contractile vessel villi are only the bulbous vesicles characteristic of this species.

Known distribution.—South Africa to Mombasa on the east coast and Île St. Paul (40°S, 80°E). All but two records are from depths less than 100 m, the deepest is at 430 m.

Golfingia elongata (Keferstein, 1863)

Phascolosoma elongatum Keferstein, 1863: 39, pl. 3, fig. 5.

Golfingia elongata.—(see Stephen and Edmonds, 1972:90–91 for most of the lengthy synonymy prior to 1970).—Åkesson, 1961:511–530.—Stephen, 1960: 15.—Murina, 1972:299; 1975:1088; 1977:215–217.—Cutler, 1973:134–136.—Zavodnik and Murina, 1975:127; 1976:85.—Gibbs, 1977:10–11.—Cutler and Cutler, 1980b:197.—Ocharan, 1980: 117–118.—Frank, 1983:11–12.—Cutler, Cutler and Nishikawa, 1984:262–263.—Saiz-Salinas, 1984:180; 1986:18–20.

Phascolosoma charcoti Hérubel, 1906a:127–128; 1906b:651–652; 1908:2–8.—Fischer, 1929:483.

Golfingia charcoti.—Stephen and Edmonds, 1972:89.

Phascolosoma cylindratum Keferstein, 1865:428.—Selenka et al., 1883:25.—Gerould, 1913:382–383.—Leroy, 1936: 425.

Golfingia cylindrata.—Stephen and Edmonds, 1972:89.

Phascolosoma derjugini Gadd, 1911:82–83.

Golfingia derjugini.—Stephen and Edmonds, 1972:90.

Golfingia ohlini.—Wesenberg-Lund, 1959b: 61.

Material examined.—MNHU, type of *G. elongata*; RSME, type of *G. cluthensis* Stephen; additional recently collected specimens from the North Atlantic.

The type material consists of several vials of specimens in very good condition, some with extended introverts showing the 8–10 rings of hooks which characterize this well founded species.

The type materials of *Golfingia charcoti*, *G. cylindrata*, and *G. derjugini* cannot be located. Cutler (1973) reduced *G. cylindrata* and Cutler and Murina (1977) reduced the other two to junior synonyms and we reaffirm those actions.

Known distribution.—From the northwest Atlantic (Newfoundland to Bermuda and Cuba), the northeast Atlantic (Spitzbergen to Iberian Peninsula and the Mediterranean) from intertidal to 200 m depths. In the Pacific from the East and South China Seas at 91–590 m. There is a single worm reported from the Indian Ocean (Mauritius intertidal sand, Wesenberg-Lund 1959b).

Golfingia iniqua (Sluiter, 1912)

Phascolosoma iniquum Sluiter, 1912:14, pl. 1, fig. 4.

Golfingia iniqua.—Stephen and Edmonds, 1972:93.

Phascolosoma mutabile Southern, 1913:19–20.

Golfingia mutabilis.—Stephen and Edmonds, 1972:101.—Murina, 1977:219–221.

Phascolosoma rugosum Southern, 1913:18–19.

Not *Phascolosoma rugosum* var. *mauritanienne* Hérubel, 1925a:262.

Golfingia rugosa.—Stephen and Edmonds, 1972:107.—Murina, 1977:219.—Saiz-Salinas, 1986:24–27.

Material examined.—Types: INMD, *G. mutabile* and *G. rugosa*; MOMV, *G. iniqua*; many recently collected specimens from near the type locality.

Cutler and Murina (1977) determined this to be a junior synonym of *G. margaritacea*. However, in light of recent comparisons of all these types (and new material) we now

believe that the earlier action was a mistake. The distinctions Southern made between his two species are probably only an artifact of size (e.g., number of tentacles) and/or state of contraction of his six individuals. His failure to compare this material to Sluiter's species may be due to the fact that they were published at about the same time. Sluiter's also were said to lack hooks while hooks are present in some (but not all) of Southern's worms. This species is one which has deciduous hooks and does share many characters with *G. margaritacea*. It is possible that future studies will show this to be a partially isolated subset of a polymorphic *G. margaritacea* gene pool (subspecies?). The major distinction lies in the shape of the trunk (more robust, fat and pear-shaped, length almost always less than 3 times the width) and the texture of the epidermis in the larger ones (over 10 mm) being thick with irregular lines/wrinkles/zig-zag pattern; admittedly somewhat less than absolute. The smaller individuals do not have as thick a body wall in the mid section but width/length ratio is consistently lower than other congeneric species.

Hérubel's (1925a) subspecies is a taxon we would place in *incertae sedis* since the description (based on a single worm of unknown size) is extremely brief, there are no illustrations, the type cannot be located, and the habitat (25 m depth at 8°24'W and 33°24'N) is atypical.

Known distribution.—Northeast Atlantic Ocean, 29–52°N, 10–30°W, from depths of 500–1800 m.

Golfingia mirabilis Murina, 1969

Golfingia mirabilis Murina, 1969:1732–1733, fig. 1.

Material examined.—Type: ZIAS.

This single worm was described as having shields but does not. The posterior end of the trunk is somewhat contracted, dark, papillated and rugose while at the anterior

end the skin has faint zig-zag ridges and is dark. The reference to a caudal appendage in the original description is somewhat misleading as the structure is 0.7 mm long on a 36 mm trunk and is really just a nipple-like termination of trunk, not uncommon in this genus. The hooks are at least 200 μ m tall and the tentacles are especially numerous, over 50 well defined units. The ventral retractor muscles originate anterior to the origins of the dorsal pair by about 10% of the trunk length, an unusual relationship within this genus. Despite the lack of an adequate data base this species seems distinct enough to be retained. There is the possibility that it is an anomalous *G. vulgaris* and if additional specimens are not collected in forthcoming years the reality of this taxon might well be questioned.

Known distribution.—Off Tanzania, 7°S, 40°E, 802 m.

Golfingia muricaudata (Southern, 1913)

Phascolosoma muricaudatum Southern, 1913:21, pl. 4, fig. 5.—Fischer, 1920:415; 1922a:10–11; 1929:483; 1931:139.

Golfingia muricaudata.—Murina, 1964:233–237; 1971:43; 1977:209–210; 1978:122.—Cutler, 1973:133–134; 1977a:140.—Cutler and Cutler, 1979:949–950; 1980a:451–452; 1980b:198–199.—Frank, 1983:13.—Cutler, Cutler and Nishikawa, 1984:265–266.

Phascolosoma appendiculatum Sato, 1934:7–10.—Murina, 1964:224–227.

Golfingia appendiculata.—Stephen and Edmonds, 1972:86.—Cutler, 1977a:139.—Murina, 1977:224–225; 1978:122.—Cutler and Cutler, 1981:60–61.—Cutler, Cutler and Nishikawa, 1984:262.

Phascolosoma hudsonianum Chamberlin, 1920:3d–4d.

Golfingia hudsoniana.—Stephen and Edmonds, 1972:91–92.

Material examined.—Types: ZMUH; numerous recently collected specimens from

near the type locality; NMCO, *G. hudsoniana*; *G. appendiculata* lost. Cutler and Cutler (1981) deposited reference specimens at NSMT and USNM which had been collected from near the type locality.

This common deep-water species is well founded. It is easily distinguished by its caudal appendage (nipple-like in very small worms to up to 50% of trunk length in large ones) bearing cylindrical papillae. The nerve cord ends anterior to the tail. Deciduous hooks (up to 100 μ m tall) are present in small individuals. The introvert is generally shorter than the trunk.

Our decision to reduce *G. appendiculata* to a junior synonym is based on our current understanding that this putative species, based on 16 worms in five records, is merely a few larger hookless individuals. Our analysis indicates that *G. muricaudata* starts its life with hooks but by the time an animal reaches 5–10 mm most have lost these deciduous structures.

Cutler (1973) determined *G. hudsoniana* to be a junior synonym and we reaffirm that conclusion.

Known distribution.—Common at bathyal and abyssal depths in the North Atlantic from Cape Hatteras (one Caribbean record at 17°N from 4000 m), up to 58°N, across to Europe and West Africa (at 60–70 m in upwelling areas off Ivory Coast). It occurs down to South Africa, Kerguelen and Bouvet Islands and up the east coast of Africa through the Mozambique Channel to Tanzania at bathyal depths. In the North Pacific it has been recorded from British Columbia around the Bering Sea to Japan at depths from 85–6860 m. Murina (1978) is the only record from the far south Pacific and is based on six worms from around 55°S, 159°E and 4400–5400 m deep. In this paper she used four names (*margaritacea*, *ohlini*, *muricaudata*, and *appendiculata*) with no morphological comments or indication of how she differentiated between these very similar forms.

Golfingia vulgaris vulgaris
(de Blainville, 1827)

Sipunculus vulgaris de Blainville, 1827:312–313, pl. 33, fig. 3 (see Stephen and Edmonds, 1972:110 for extensive synonymy prior to 1970).

Golfingia vulgaris.—Murina, 1971:43; 1973:70; 1977:217–219.—Zavodnik and Murina, 1975:128; 1976:85–86.—Cutler and Murina, 1977:177–178.—Gibbs, 1977:14–15.—Cutler and Cutler, 1979a:950.—Frank, 1983:13–14.—Cutler, Cutler and Nishikawa, 1984:266–267.—Saiz-Salinas, 1986:27–29.

Phascolosoma vulgare var. *astuta* Selenka, 1885:11.

Golfingia vulgaris astuta.—Stephen and Edmonds, 1972:111–112.

Phascolosoma vulgare var. *multipapillosum* Hérubel, 1925a:261.

Golfingia vulgaris multipapillosa.—Stephen and Edmonds, 1972:112.

Phascolosoma vulgare selenkae Lanchester, 1905:31–32.

Golfingia vulgaris selenkae.—Stephen and Edmonds, 1972:112–113.

Phascolosoma vulgare tropicum Sluiter, 1902:33–34.

Golfingia vulgaris tropica.—Stephen and Edmonds, 1972:113.

Golfingia (Dushana) adriatica Murina, 1975:1085–1087.—Zavodnik and Murina, 1976:86.

Phascolosoma kolense Gadd, 1911:80–81, 102–103.

Golfingia kolensis.—Stephen and Edmonds, 1972:93.—Cutler and Murina, 1977:177–178.

Phascolosoma owstoni Ikeda, 1904:12–15.

Golfingia owstoni.—Stephen and Edmonds, 1972:103–104.—Murina, 1977:214–215.—Cutler and Cutler, 1981:64–65.

Phascolosoma solitarium Sluiter, 1912:15–16.

Golfingia solitaria.—Stephen and Edmonds, 1972:108.—Murina, 1977:227.

Not *Golfingia vulgaris* [sic] var. *antarctica* Murina, 1957:996–997 (= *Golfingia vulgaris murinae* nom. nov. pro Stephen and Edmonds, 1972:111) (see *G. margaritacea ohlini*).

Material examined.—Types: MOMV, *G. solitaria*; ZMUA, *G. v. tropica*; BMNH, *G. v. astuta* and *G. v. selenkae*; ZIAS, *G. adriatica*. Types of *G. vulgaris*, *G. kolensis*, *G. owstoni*, and *G. v. multipapillosum* cannot be located.

This is a common, well-founded species characterized by both ends of the trunk distinct, much darker and more heavily papillated than the mid-trunk. The introvert is shorter than the trunk and it has normal tentacles. The large hooks are scattered, dark and spine-like. Its spindle muscle is well developed and originates under the wing muscle just posterior to the anus, sometimes from two branches.

Selenka's variety *astuta* is represented by a single, dried, collapsed, hard worm which precludes any internal examination. There are no external features to distinguish it from *G. vulgaris*, therefore, we reduce this individual to the status of a junior synonym.

When Hérubel (1925a) used the name *Phascolosoma vulgare multipapillosum* he provided neither a description nor illustration. It was merely listed along with two other subspecies and consequently this has no meaning.

The two *G. v. selenkae* Lanchester described from East Africa are in good condition. However, the alleged differences are not significant (hook and papillae size, and origin of the ventral retractor muscles); these fall within the range for this species. At this time the animals do not show any indication of the dark pigment on the ends of the trunk so typical of this species. Rather, they are a uniform light brown color. Its shallow, tropical location is more noteworthy than its morphology.

Sluiter's (1902) subspecies, *G. v. tropica* was based on two worms. One of these is a *Nephasoma* species. The alleged distinc-

tions of the remaining worm from the nominate form are within the range of variation and judged to be insignificant. Sato's (1934) use of this name was because of the hook size (60–70 μm), now known to be normal for the species.

Golfingia adriatica was based on two specimens, each lacking one dorsal retractor muscle and possessing an inner body wall with peculiar connective tissue sheets (partial dissepiments). The subgenus erected at this time was defined as having 'shields' at both ends of the trunk but this is another problem of semantics (see Introduction). The type species for the subgenus was *G. scutiger* (see below). It is clear to us that these two worms are anomalous *G. vulgaris* with ontogenetically modified retractor muscles as noted in other species (see Gibbs 1973).

Golfingia kolense (Gadd, 1911) was synonymized by Cutler and Murina (1977). *Golfingia owstoni* was discussed in Cutler and Cutler (1981:64–65) where they concluded that the alleged differences were insignificant.

The single specimen of *G. solitaria* is in good condition. It does lack hooks, the contractile vessel is bulbous, and there are prominent papillae on both ends of the trunk. No additional specimens have been recorded from the North Sea or adjacent waters and we propose that Sluiter's worm is simply one hookless representative of this population and therefore a junior synonym.

Known distribution.—In the Northeast Atlantic Ocean including Greenland, Scandinavia, the British Isles, and into the Mediterranean, Adriatic and Red Seas; south to the Azores, Canaries, and Cape Verde Islands and West Africa; in the Indian Ocean off Durban and Zanzibar; the Pacific Ocean in the Kurile-Kamchatka Trench, Japan, Malaya, Singapore and one record (Frank 1983) off British Columbia (the only one from the eastern Pacific). The total depth range is from 5–2000 m but more commonly 10–500 m, deeper records are rare. There is one very deep record from 5540 m

in the Kurile-Kamchatka Trench. Its absence from the western Atlantic ocean and rarity in the eastern Pacific Ocean is noteworthy. The Indo-West Pacific warm water records may belong to a distinct population (or the following subspecies?) but there is currently insufficient data to assert this with confidence.

Golfingia vulgaris herdmani
(Shiple, 1903) new status

Centrosiphon herdmani Shiple, 1903:171–174, pl. 1, figs. 4–10.—Stephen and Edmonds, 1972:268–269.

Golfingia herdmani Edmonds, 1980:19–21.

Golfingia liochros Cutler and Cutler, 1979a: 950–951, fig. 2.

Golfingia (Golfingia), n. sp. Cutler, 1977a: 140.

Golfingia vulgaris queenslandensis Edmonds, 1956:303–305.—Stephen and Edmonds, 1972:112.—Edmonds, 1980: 21–22.

Material examined.—The type (and only) material of *Centrosiphon herdmani* cannot be located but several recently collected Australian specimens identified by Edmonds as *G. herdmani* were examined; AMSS, Type of *G. v. queenslandensis*; MNHN, Type of *G. liochros*.

This taxon differs from the nominate form by having the anterior and posterior ends of the trunk forming a modified cap or pseudoshield consisting of dark spherical papillae arranged in irregular radiating rows especially evident on the posterior end. It also has larger hooks (120–200 μm) associated with bulbous papillae and lives in shallow warm water.

Edmonds' account of *G. herdmani* is detailed and precise. In the thirty years since *G. v. queenslandensis* was described no new material has been given this name. One of the major distinguishing features of *G. herdmani* is the peculiar nature of the anterior and posterior trunk; “. . . looking rather like aspidosiphonid caps or shields which are

surrounded at their junction with trunk by a fold of body wall.” However, when describing this species Edmonds (1980:19) went on to say “When the specimens are relaxed the “shields” usually become less evident and sometimes disappear.” In *G. v. queenslandensis* he said: “There is a weakly developed rim between the base of the introvert and the trunk, much like that found in *G. herdmani*” (Edmonds 1980:22), therefore, in our opinion, simply two relaxed specimens of the same species. These two worms are paler but the arrangement of the posterior papillae is the same. His comment that the *G. herdmani* are internally very similar to an Australian subspecies of *G. margaritacea* is true but the same could be said for many members of this genus.

The original description of *G. liochros* compared it to two species with ‘shields’ now considered to be junior synonyms of *G. vulgaris*. There are external similarities to *G. v. vulgaris* but differences sufficient to retain its separate status were believed to be present. After this side-by-side comparison it is clear we were mistaken. Some worms do have bulbous contractile vessels and the size of the ventral retractors may vary from 1.5–4 times the ventral (usually 2–3). Other size-related differences we have covered in the introduction to this paper. As these worms are less than 20 mm long and the *G. v. herdmani/queenslandensis* are up to 60 mm and since all exist around the Indian Ocean we conclude that we simply have the two ends of one continuum; i.e., a shallow water Indo-West Pacific taxon.

Known distribution.—Madagascar, Mozambique Channel, Ceylon, Thailand, Great Barrier Reef and South Australia from intertidal depths (one at 300 m).

Species Transferred to Other Genera in
Previous Papers

These species are listed with only brief comments. Additional details can be found in the cited references.

Golfingia recondita (Sluiter, 1900)

This was transferred to the subgenus *Mitosiphon* in Cutler and Murina (1977). In Cutler (1979) this was shifted to the subgenus *Apionsoma* which has since been elevated to generic rank (Cutler and Gibbs 1985). It is not a well founded species.

Golfingia trichocephala (Sluiter, 1902)

This followed a path similar to that of *G. recondita* except that the first shift occurred in Cutler (1973) when it was moved to the subgenus *Mitosiphon*. It is presently in the genus *Apionsoma* (Cutler 1979) and is a widespread, common species.

Species Considered *species inquirendum* or *incertae sedis**Golfingia reticulata* (Hérubel, 1925)

Phascolosoma reticulatum Hérubel, 1925a: 262; 1925b:272–277, text-figs. 1–6.

Golfingia reticulata. — Stephen and Edmonds, 1972:105–107. — Saiz-Salinas, 1986:22–24.

Material examined. — Type: MNHN.

The single type specimen is in very bad condition, partially dried out and the introvert is missing so we cannot verify any of the critical differences. The area around the type locality has been intensely sampled over the past few decades and nothing matching this description has been collected. Saiz-Salinas (1986) merely repeated the original record. Several aspects of the description are peculiar but in many ways this is similar to *G. vulgaris*. In our judgment it is best to add this name to the list of *incertae sedis*.

Golfingia scutiger (Roule, 1906)

Phascolosoma scutiger Roule, 1906:81–86, pl. 9, figs. 90, 95, 96, pl. 10, figs. 97–99.

Golfingia scutiger. — Murina, 1975:1085–1089; 1977:212.

Material examined. — Type cannot be located.

This single specimen from the coast of Morocco was omitted from Stephen and Edmonds (1972). The worm seems to have been lost to science and no one has applied this name to additional material since 1906. We strongly suspect that this is a specimen of *G. vulgaris* with the posterior end drawn in and flattened, but since we cannot verify this we hereby place it on the list of *incertae sedis*. Murina (1975) unfortunately used this enigmatic taxon as the type species for her new subgenus *Golfingia (Dushana)* which now ceases to have any meaning (see also *G. adriatica*).

Golfingia anguinea (Sluiter, 1902)

Phascolosoma anguineum Sluiter, 1902:36–37, pl. 3, figs. 13–16.

Golfingia anguinea. — Stephen and Edmonds, 1972:85.

Material examined. — Type: ZMUA.

The single specimen is in very poor condition. The internal organs are missing or badly distorted. The introvert was described as being four times the trunk length but it now appears torn and incomplete and is only equal to the trunk in length. The description of this introvert tip with “thread-like feeler” sounds like a ripped introvert, not the natural state. As the poor condition of this specimen precludes verification of the description and no additional specimens have been recorded, we place this name on the list of *species inquirendum* pending future clarification.

Golfingia lagensis (Fischer, 1895)

Phascolosoma lagense Fischer, 1895:13–14; 1914:76–77, pl. 2, figs. 1–3.

Golfingia lagensis. — Stephen and Edmonds, 1972:93–94.

Material examined. — Type cannot be located.

This species was based on a single 10 mm specimen which seems to have been lost to science. The presumed absence of a spindle muscle has been heavily weighted (Stephen and Edmonds 1972) but the fact that Fischer was "unable to perceive" this fine thread-like muscle in a single small worm is not surprising (see Introduction). One could place this in synonymy with *G. margaritacea* based on overall similarity as Wesenberg-Lund (1959a:209) suggested, but a more prudent option, being unable to verify anything about this specimen, is to place it on the list of *incertae sedis*.

Acknowledgments

The continued interest and exchange of ideas with S. Edmonds, Adelaide, and P. Gibbs, Plymouth, have been invaluable. We are indebted to G. Brown, Utica College, who did much of the analysis of the literature on *G. margaritacea* and to G. C. Steyskal, Washington, who kindly provided guidance in emending the species names. Financial support was provided by the National Science Foundation (grant BSR 83-14301). The cooperation of the following persons and institutions in the loan of reference material and/or providing access to their collections was essential to the completion of this project and is appreciated: P. Hutchings (AMSS); R. Sims (BMNH); Irish National Museum, Dublin; J. Renaud-Morant (MNHN); G. Hartwich (MNHU); G. Testa (MOMV); R. Oleröd (NHRS); National Museum of Canada, Ottawa; S. Chambers (RSME); University Museum, Oxford University; M. Rice (USNM); J. Kirkegaard (UZMK); A. V. Ivanov (ZIAS); Zoological Institute Tohoku University, Sendai; Institut voor Taxonomische Zoologie, Amsterdam; E. Willassen (ZMUB); M. Dzwillo (ZMUH).

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